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Sandy beaches as biogeochemical hotspots: the metabolic role of macroalgal wrack on low-productive shores[1]

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Abstract

Sandy beaches, which represent the most common type of land-sea interface, harbour distinctive biotic communities and regulate the flow of energy between marine and terrestrial ecosystems. Accumulations of sea wrack on sandy beaches are of crucial importance for recycling beach nutrients and for regulating trophic connectivity and coastal functioning. We investigated the role of beaches as biogeochemical hotspots by examining the metabolic activity in accumulations of different species of wrack on two exposed beaches affected by different levels of human pressure. Experimental wrack patches provided large amounts of different sedimentary nutrients over time due to remineralization of the algae. Unsurprisingly, the variation in the nutrients present in the beach sediments was related to the species of wrack considered. Macroalgal wrack was metabolically very active and supported high respiration rates represented by intense CO_2 fluxes. Importantly, we demonstrated that the wrack metabolic rate differed significantly depending on the algal species considered. Different macrofauna and bacterial assemblages were identified in the different wrack patches and on the different beaches. We suggest that human activities such as beach grooming can modify the wrack-associated communities, thus contributing to the variability in the biogeochemical processes and metabolic rates. Significant changes in the type and amount of wrack deposited on beaches can change fundamental processes related to the marine-terrestrial transfer of nutrients and energy and to the marine-atmospheric transfer of CO_2 emissions, with ecological consequences for nearshore environments.

Keywords: bacterial assemblages; benthic macrofauna; CO_2 emissions; metabolic hotspots; non-native species; nutrient inputs

1. Introduction

Sandy beaches are valuable ecosystems that provide ecological and socioeconomic services such as provision of harvestable resources, recycling of organic matter and nutrients, coastal protection and social recreation (Schlacher and others 2008). They are also natural habitats for many distinctive plants and animals, and as transition zones can be colonized by highly diverse and unique biological communities (Schlacher and others 2008). These different components interact in a large ecological network to create the open ecosystems of sandy beaches. Sandy beaches represent the main interface between marine and terrestrial ecosystems and regulate exchanges between these key systems, thus contributing to the normal functioning of both (e.g. Dugan and others 2003; Lastra and others 2008; Spiller and others 2010).

The spatial input of nutrients via the movement or deposition of organisms or material on shorelines around the world is of key significance for relatively unproductive coastal ecosystems such as exposed beaches. This pattern has been increasingly studied in recent years (e.g. Inglis 1989; Dugan and others 2003; Ince and others 2007; Lastra and others 2008; Crawley and others 2009; Rodil and others 2015a,b). Macrophytes become naturally detached from rocky shores and subtidal bottom habitats and transported to nearby beaches where they accumulate and decompose as wrack for variable amounts of time (Orr and others 2005; Mews and others 2006). Wrack deposits have the potential to provide rich and highly heterogeneous habitats for a range of organisms, including marine and terrestrial macroinvertebrates and also microbial communities (Colombini and Chelazzi 2003). Furthermore, by providing external food sources to beaches, wrack becomes an important vehicle of carbon and nutrient exchange between different aquatic ecosystems and between marine and terrestrial ecosystems (Dugan and others 2011; Spiller and others 2010). Wrack that is deposited across the entire intertidal range is moved by tides and waves

before being washed away. However, wrack accumulations may remain, age and decompose on the supratidal areas for several weeks and are often buried, thus affecting the physical and chemical characteristics of the sediments for a long period (Orr and others 2005). Wrack will thus decay and release nutrients into the sediment, stimulating the growth of bacteria, supplying organic matter for the macrobenthos and modifying oxygen exchange in the sediment (Dugan and others 2011). Typical benthic communities (i.e. bacteria, meio- and macrofauna) also play a key role in the decomposition and transformation of wrack through fragmentation, decomposition and remineralization (Lastra and others 2008; Dugan and others 2011). These processes will depend on the quantity and quality of the wrack as well as on the frequency and spatial distribution of the accumulations (e.g. Orr and others 2005; Mews and others 2006; Olabarria and others 2007; Rodil and others 2008). Most studies of beach wrack have focused on the surface of sediments, and the effects of buried wrack have received only incidental attention (e.g. Olabarria and others 2010; Pelletier and others 2011). Moreover, most studies have focused on the fauna, with little consideration given to the metabolism of the community thriving on these deposits, which is likely to be dominated by microbial communities. For example, bacteria are responsible for remineralizing most of the detritus back into nutrients, thus playing a key role in the functioning of nearshores (Koop and others 1982, Inglis 1989).

Interfaces between terrestrial and aquatic ecosystems have been recognized as biogeochemical hotspots (*sensu* McClain and others 2003), and recent evidence shows that sandy beaches fit this concept for nutrient cycling (Dugan and others 2011). Beach wrack deposits can be considered metabolic hotspots with high activity and rates of CO_2 flux relative to other marine and terrestrial habitats (Coupland and others 2007). Community respiration may be a good indicator of the flow of organic matter in ecosystems (Williams

and del Giorgio 2005). Thus, intense respiration reveals an active metabolic role of wrack material, whereas low respiration rates suggest that the material accumulated has a largely structural role (Coupland and others 2007). The metabolic activity of beach wrack has not been studied in detail, although it is the foundation for thriving life and the development of diversity in such environments characterized by low productivity (see Coupland and others 2007). The biogeochemical processes associated with wrack must be investigated in order to improve our understanding of the ecological role of these spatial deposits in supporting the basic processes of nutrient remineralization and beach functioning (Dugan and others 2011). The role of these processes may vary depending on the beach considered and on the intensity of human impact. For instance, wrack is often removed mechanically from tourist beaches, thus significantly reducing the amounts of organic matter in shoreline sediments, offshore nutrient concentrations, and microbial and macrofauna numbers in the terrestrial and aquatic parts of the beach ecosystem (e.g. Dugan and others 2003; Malm and others 2004; Russell and others 2014).

We considered whether two ocean-exposed sandy beaches act as biogeochemical hotspots (McClain and others 2003) by extending the hotspot concept to wrack deposits. We deliberately buried macroalgal detritus to test the fate and the respiration rates supported by beach wrack and to examine changes in the sedimentary biogeochemical composition. Specifically, we compared *in situ* respiratory CO_2 fluxes in four macroalgal species, and we described how the different types of wrack affected the nutrient composition and respiratory rates in the sediment over time. In addition, we examined the role of macrofaunal and bacterial assemblages in the wrack metabolic activity and nutrient remineralization by comparing the existing relationships between sedimentary changes and beach benthic communities. We performed the study on two sandy beaches affected by different types of human activity to examine different ecological responses associated with

118 different anthropogenic impacts.

119 **2. Material and methods**

120 **2.1. Study sites, experimental design and set-up**

121 The study was conducted at two nearby beaches: América (AM) and Abra (AB)
122 beaches, which are typical of exposed sandy beaches on the NW coast of Spain. Both
123 beaches are influenced by a mesotidal regime with a medium tidal range of ~3.5 m. AM
124 beach (42º 7' 53" N, 8º 49' 83" W), which is about 1280 m long and 103 m wide (low
125 spring tide), is located in an urbanized area that receives large numbers of tourists during
126 weekends and summer. The beach has a well-developed seafront promenade, and a dune
127 habitat rehabilitation project was initiated in 2005 in some areas between the promenade
128 and the beach. The abundance of macroinvertebrates on AM beach is generally low, and
129 supratidal macrofauna is rarely found (De la Huz and others 2005). AM beach is subjected
130 to frequent mechanical grooming (i.e. daily during summer and holidays and occasionally
131 during the rest of the year) to remove accumulations of detritus from the ocean, including
132 wrack (pers. obs). AB beach (42º 9' 11" N, 8º 49' 49" W), which is about 225 m long and
133 40 m wide, is located in an urbanized area, but is relatively isolated from visitors. The dune
134 habitat is non-existent and the space is occupied by old houses and a seawall.
135 Invertebrates, such as amphipods, are abundant on the beach (pers. obs.). Mechanical
136 grooming to remove debris is not currently carried out on the beach (pers. obs.).

137 Despite the difference in the dimensions, these two neighboring beaches are exposed to
138 similar oceanographic conditions and receive similar deposits of algal wrack species
139 (Barreiro and others 2011). Thus, wrack is naturally very abundant, diverse and variable on
140 both beaches (supplementary material Figure S1), with patches mainly composed of brown
141 algae spread through the beach shore (Barreiro and others 2011, 2013). Three days before
142 the start of the experiment, entire fresh portions of four of the most abundant brown

143 macroalgal species found on this coastline (Olabarria and others 2009; Barreiro and others
144 2011, 2013) were collected. Two native species *Saccorhiza polyschides* (Lightfoot)
145 Batters, 1902 (hereafter Sp) and *Cystoseira baccata* (S. G. Gmelin) P. C. Silva, 1952 (Cb),
146 and two non-native species *Sargassum muticum* (Yendo) Fensholt, 1955 (Sm) and
147 *Undaria pinnatifida* (Harvey) Suringar, 1873 (Up) were collected by hand from nearby
148 rocky areas, transported to the laboratory, separated into patches of similar weight (1.0 ±
149 0.1 kg wet weight) and stored in bags while the decomposition process began. We used a
150 standardized, manageable quantity of wrack that was sufficient to trigger both microbial
151 degradation of the wrack and the macrofaunal colonization processes (Olabarria and others
152 2007; Rodil and others 2015a,b). We included non-native species because they are
153 increasingly abundant on shores around the world, with important ecological and
154 economic effects on coastal systems (e.g. Rodil and others 2008; Williams and Smith
155 2007; Suárez-Jiménez and others 2017).
156 The experiment began on 13 March 2015 (time 0) and lasted for 12 days, i.e. a
157 sufficient length of time for the wrack degradation and community colonization process to
158 occur (Olabarria and others 2007; Rodil and others 2008; Lavery and others 2013).
159 Experimental patches of each algal species (n = 4) were placed in previously dug (10 cm
160 depth), square holes (0.25 m^2) and were covered with a fine layer of sand (1-2 cm). The
161 spacing between each patch was 2 m apart, and the location was determined by random
162 distribution. On days 3, 6, and 12, four randomly chosen replicate patches were sampled
163 on each beach. Thus, a total of forty-eight patches of wrack were placed on each beach at
164 the highest mark of the drift line parallel to the shoreline (i.e. 4 algal species x 3 days x 4
165 replicates). Procedural sand controls (PC, n = 4), in which the sediment was disturbed but
166 no wrack was added, were established. Wrack degradation, which rapidly affects
167 sedimentary traits, nutrient recycling and community structure of beaches, is dependent on

168 the algal species (Lavery and others 2013; Rodil and others 2015a,b). On day 12, all wrack
169 patches left on AB were washed away due to an extremely high spring tide (augmented by
170 a solar eclipse and a *perigee* full moon).

171 **2.2. Sediment and nutrient analyses**

172 Sediment samples were randomly collected from underneath each wrack patch to
173 measure sedimentary water content, organic matter and nutrient contents. The water
174 content (%) of sediment samples (~80 g) was calculated as the difference between the
175 initial wet weight and the final dry weight (60ºC, 24 h). Total organic matter (OM, %)
176 was measured as the difference in the weight of sediment (~ 50 g) before and after
177 ignition (500 °C, 4 h). The inorganic dissolved nutrients in sediments (± 20 g) were
178 filtered (2-4 μm filter paper) to remove any particulate material and stored at −30°C.
179 The nutrients were quantified by continuous flow analysis (CFA) in Auto-Analyzer
180 (Bran Luebbe AA3). The Berthelot reaction was used to determine the ammonium
181 concentration (NH_4^+) (absorbance at 660 nm); nitrites (NO_2^-) were determined by the
182 sulphanylamide and N-1-napthylethyleneidiamine dihydrochloride reaction (550 nm);
183 nitrates (NO_3^-) were converted to NO_2^- and measured as above. Phosphates (PO_4^{-3}) were
184 determined by the ammonium molybdate and ascorbic acid reaction (880 nm).

185 **2.3. Wrack metabolic activity**

186 Estimates of CO_2 effluxes (μmoles m^{-2} day^{-1}) were measured *in situ* in the middle of
187 each wrack patch using a portable soil respiration gas analyzer (WEST Systems
188 fluxmeter®). This device, which includes a metallic cylindrical respiration chamber (cover
189 area 500 cm^2), allows measurement of fluxes in 2-3 minutes based on the rate of
190 accumulation of CO_2 within the chamber. On days 0 (4 random replicates of freshly
191 allocated algae), 3, 6 and 12 of the study, the chamber was inserted (approx. 2cm) into the

192 wrack deposit in each corresponding experimental patch by applying gentle pressure to the
193 top of the chamber. Wrack temperature was simultaneously measured with an alcohol
194 thermometer (°C). The fluxes were always measured between 10:00 and 12:00 (solar
195 time), because mid-day values of CO_2 efflux have been shown to be representative of daily
196 averages (Xu and Qi, 2001). Immediately after the measurements, we excised the wrack
197 area below the flux chamber (i.e. 500 cm^2) with a cutter. The excised portions were placed
198 in plastic bags, transported to the laboratory and frozen (- 20ºC). All the macrofauna
199 associated with the excised wrack portions were separated and preserved in ethanol (70%)
200 for later identification. All the excised wrack portions were dried (60ºC, 48 h) and weighed
201 (g) to estimate the change in wrack biomass over time.

202 **2.4. Wrack-associated bacterial community structure**

203 Sediment samples were randomly collected to evaluate bacterial communities by
204 Automated-rRNA Intergenic Spacer Analysis (ARISA). This technique exploits the
205 variability in the length of the intergenic spacer (IGS) between the small (16S) and large
206 (23S) subunit rRNA genes in the rrn operon (Ranjard and others 2001). The DNA was
207 amplified using ITSF (5′GTCGTAACAAGGTAGCCGTA-3′) and ITSReub (5′-
208 GCCAAGGCATCCACC-3′) primer sets (Cardinale and others 2004), to amplify the ITS1
209 region in the rRNA. Total DNA was extracted from 1.0 g wet weight of homogenized
210 subsamples by using the Power Soil Extraction Kit (Mo Bio Laboratories, Inc). PCRs were
211 performed in triplicate 25 mL volumes containing between 5 and 50 ng of DNA, 400 mM
212 of both primers, 0.3 mM dNTPs, 3 x Taq PCR buffer, 2.5 U Taq DNA polymerase, 2.5
213 mM $MgSO_4$ and 1 mg mL^{-1} serum albumin (BSA). A standardized amount of the product
214 was diluted 1:5 and mixed with 0.5 µL of ROX-labelled genotyping internal size standard
215 (ROX 1000, Applied Biosystems). The sample fragments were analyzed in a genetic
216 analyzer (ABI3730 XL).

ARISA fragment lengths were analyzed using Peak Scanner Software (Applied Biosystems). Fragments that differed by less or equal to 2 base pair (bp) were considered identical, and fragments with Fluorescence Units below 50 were considered "background noise". Fragments > 200 bp were considered too short ITS for bacteria and removed. The bacterial richness was estimated as the total number of unique operational technical units (OTUs) identified within each electropherogram (see supplementary material, Figs. S2-S3), where the number of peaks represented the species number (phylotype/genotype richness), and the peak height (fluorescence units) represented the relative abundance of each bacterial species. The Shannon–Wiener diversity index, which considers the number of species present and their relative importance within the assemblage, was calculated using the PRIMER S/W (Clarke and Gorley, 2006).

2.5. Wrack-associated macrofauna community

Samples of macrofauna were collected under each experimental patch with a 10-cm diameter corer (n = 3), penetrating 20 cm deep into the substratum. The samples were enclosed in individually labelled plastic bags, before being transported to the laboratory. The individuals were sorted, identified and counted to the lowest possible taxonomic level. Macroinfauna collected from the sediment and all the macrofauna associated with the excised wrack portions (see section 2.3.) were pooled to obtain total abundance (i.e. counts) and the number of taxa per experimental patch, and used as the main benthic community descriptors.

2.6. Statistical analysis

Changes in wrack temperature, biomass and metabolic activity (i.e. CO_2), and changes in sediment water content, organic matter and inorganic nutrient concentrations were analyzed using 3-way ANOVA models. A Type II Sum of Squares ANOVA

241 (Langsrud, 2003) was used to deal with unbalanced data (i.e. missing data from AB day
242 12). Beach (AM and AB), patch (Sp, Up, Cb, Sm, PC), and time (t3, t6, and t12 days, or
243 t0, t3, t6 and t12 days for CO_2) were considered orthogonal fixed factors. Changes in
244 bacterial richness (OTUs) were analyzed using the same models. The normality
245 (Shapiro test) and the variance (Levene's test) of the residuals were evaluated, and Box-
246 Cox power transformations were performed when necessary. Three factor non-
247 parametric multivariate analysis of variance (PERMANOVA, PRIMER S/W) was used
248 to examine differences between bacterial assemblages (Anderson and others 2008). The
249 data were normalized by presence/absence before being analyzed using a Bray-Curtis
250 resemblance matrix (4999 permutations). Significant effects identified were further
251 investigated by pairwise comparisons. Non-metric multidimensional scaling (nMDS,
252 PRIMER S/W) was used to visualize multivariate patterns in bacterial assemblages.
253 Changes in macrofauna were analyzed by use of generalized linear models (G_zLM), due
254 to the large number of zero values. *A posteriori* comparisons were performed using the
255 least squares means (lsmeans) package (Lenth 2016) and Tukey's adjustment.
256 We used G_zLM to examine the relationships between the main benthic community
257 descriptors (i.e. bacterial diversity, OTUs and macrofauna abundance) and the biomass,
258 metabolic activity and nutrient release from the wrack. We included the same
259 categorical factors as above and the main benthic community descriptors (as co-
260 variables) as the predictor variables, and considered wrack biomass (i.e. dry weight),
261 metabolic activity (i.e. CO_2) and sedimentary traits (i.e. water content, organic matter
262 and inorganic nutrients) response variables. We first fitted maximal models using all the
263 factors and descriptors (variance inflation factor < 2) to check for interactions between
264 factors and continuous predictors. We simplified the models by removing non-
265 significant interaction terms and non-significant explanatory variables. The Akaike's

Information Criterion (AIC) and the proportional increase in explained deviance (pseudo-R^2) were used to evaluate each model fit. *A posteriori* comparisons were performed by reassigning the "Intercept" term sequentially and using lsmeans. The following model assumptions were checked: (i) homogeneity, by examining plots of residuals against fitted values; (ii) normality, by examining quantile-quantile plots or histograms of the residuals; and (iii) data independence, by examining plots of residuals against each explanatory variable. All statistical analyses were performed with R software (R Development Core Team, 2016).

3. Results

3.1. Ambient conditions within experimental wrack patches

Wrack biomass decreased over time (t3 > t6 > t12; $p < 0.001$), with significant ($p < 0.001$) differences between algal species (Sm = Cb > Sp = Up) (Figure 1a-b, Table S1). Wrack temperature varied significantly over time on AM beach (t3 < t6 > t12), and it was higher ($p < 0.001$) in patches on AB than on AM (Figure 1c, Table S1). The sedimentary organic matter content was higher ($p < 0.001$) in patches of Up at t12 than in the patches of the other wrack species (Figure 1d, Table S1). Water sediment differed ($p < 0.001$) between beaches (AM > AB) and between patches (Up > Sp = Sm > Cb > Sand) (Figure 1e-f, Table S1).

3.2. Nutrient analysis of the sediments under patches

The concentrations of inorganic dissolved nutrients, i.e. NO_2^-, NO_3^-, NH_4^+, and PO_4^{3-}, varied between patches, and patterns differed between beaches and over time (Figure 2, Figure 3, Table S2). Thus, the concentration of NO_2^- under Sp was higher ($p < 0.001$) than under any other patch, except for Up on AB (Figure 2a). The NO_2^- concentration increased significantly ($p < 0.001$) over time, only in the Sp patch (t3 < t6 = t12; Figure

290 3a). The NO_3^- concentration differed significantly ($p < 0.001$) between patches on AM
291 beach (Sp > Up = Cb =Sm > Sand) and on AB beach (Sp = Up > Cb = Sm > Sand)
292 (Figure 2b). The concentration of NO_3^- under Sp increased significantly ($p < 0.001$)
293 over time (t3 < t6 = t12) (Figure 3b). The concentration of NH_4^+ differed significantly
294 ($p < 0.05$) between wrack and the bare sand (control) on AM beach (Figure 2c) and at
295 t12 (Figure 3c). No significant differences in NH_4^+ concentrations were found on AB
296 (Figure 2c). The concentration of PO_4^{3-} was significantly higher ($p < 0.001$) in the Up
297 patches than in other patches on AM and AB (Figure 2d) on all sampling dates (Figure
298 3d). The concentration of PO_4^{3-} in the Sp and Sm patches on AM and in the Cb patches
299 on AB were significantly higher than in the bare sand (Figure 2d). The concentration of
300 PO_4^{3-} increased significantly ($p < 0.001$) over time in both the Sp (t3 < t6 = t12) and Sm
301 (t3 = t6 < t12) patches (Figure 3d).

302 **3.3. Wrack metabolic activity**

303 The experimental wrack patches supported high metabolic activities, as reflected by
304 the accumulated CO_2 fluxes: (mean ± SE) 3.5 ± 0.4 on AM and 4.2 ± 0.6 on AB (μmol
305 CO_2 m^{-2} s^{-1}), compared to the mean value of 0.1 μmol CO_2 m^{-2} s^{-1} for the bare sand
306 control (Table 1). The first wrack metabolic measurements (t0) already showed a
307 significant response relative to bare sand (Figure 4, Table 2). The metabolic rates varied
308 significantly ($p < 0.001$) between patches, between beaches and over time (i.e. triple
309 interaction, $F_{8,105} = 4.8$) (Table S2). Thus, the metabolic activity in Sp was very high
310 and increased significantly ($p < 0.001$) over time on AM and AB, although it was
311 significantly lower ($p < 0.001$) at t12 in the Sp patch on AM (Figure 4, Table 2). The
312 metabolic activity was higher in Up than in the other types of wrack (see t3 for both
313 beaches) between patches ($p < 0.001$) and over time (Figure 4) on AM and AB (Table

2). The metabolic activity was lower in the Cb patches than in the other patches at all times (Figure 4). The metabolic rate in Cb patches on both beaches increased significantly ($p < 0.001$) after six days (Figure 4, Table 2). The metabolic rate in the Sm patches increased significantly ($p < 0.001$) after 12 days on AM and after 6 days on AB (Figure 4). The only significant difference ($p < 0.01$) between beaches in relation to the metabolic activity (AM < AB) was observed for Sm (AM: 0.528 ± 0.066 µmoles m^{-2} s^{-1} and AB: 1.467 ± 0.229 µmoles m^{-2} s^{-1}; mean±SE) at t3 (Figure 4, Table S3).

3.4. Wrack-associated communities: bacterial and macrofaunal characterization

Bacterial relative abundance and richness ranged respectively from 862 to 298 150 fluorescence units (peak heights) and from 11 to 268 OTUs (Figures S2-S3). The presence of wrack increased the richness ($F_{4,75} = 2.6$; $p < 0.05$) of bacteria relative to the bare sand. OTUs richness increased over time at AM (t3 < t6, t3 < t12; p < 0.01 and t12 < t6; $p < 0.05$) and AB (t3< t6; $p < 0.001$) (Figure 5a, Table S4). The similarity in the wrack-associated bacterial assemblages between beaches was low, but significant (33.4%, t = 4.2; p < 0.001). The assemblages varied significantly between patches, between beaches and over time (pseudo-$F_{1,75} = 4.8$; $p < 0.001$). Thus, Sp and Up showed the lowest similarities on AM, and Sm showed the lowest similarities to the other patches on AB (Figure 6, Table S5,). The bacterial assemblages within patches of the same wrack species showed lower similarity on AM than at AB over time (Table S5, Figure 6).

A total of 1,969 macroinvertebrates from 9 taxa were identified (Table S6). The number of taxa (AM: t3 = t6 < t12, AB: t6 < t12) and abundance (t3 = t6 < t12) associated with wrack increased significantly ($p < 0.001$) over time (Table S4). However, the number of taxa was significantly larger ($p < 0.001$) on AB than on AM (Figure 5b). Abundance differed significantly between wrack patches on AB (Table S4,

Figure 5c). Most organisms sampled on AM were dipteran larvae belonging to the Anthomyiidae family ($p < 0.001$), and most specimens from AB were amphipods (Talitridae family) ($p < 0.001$). The abundance of Anthomyiidae differed significantly ($p < 0.001$) between patches on AM (Sp = Cb > Up = Sm) and AB (Cb > Sp > Up = Sm) (Figure 5d), and it increased ($p < 0.001$) over time (t3 = t6 < t12). The abundance of Talitridae differed significantly between patches, but only on AB (Cb = Sm > Sp = Up = Sand; $p < 0.001$) (Figure 5e).

3.5. Relationships between wrack-related variables and community descriptors

Bacterial richness (OTUs) was significantly ($p < 0.01$) and negatively (Estimate = -0.003, t = -2.9; pseudo-R^2 = 59.1) related to wrack biomass ($F_{1,74} = 8.85$; $p < 0.01$) (Figure 7a). Bacterial diversity (Shannon-Wiener index) was significantly ($p < 0.05$) and positively (Estimate = 0.22, t = 3.3; pseudo-R^2 = 24.1) related to the sedimentary dissolved inorganic nitrogen (i.e. DIN = NO_2^-+ NO_3^- +NH_4^+) under the wrack patches ($F_{1,73} = 11.2$; $p = 0.0013$) (Figure 7b).

Macrofaunal abundance was significantly and positively related to both organic matter ($F_{1,97} = 4.9$; $p < 0.05$) and NH_4^+ ($F_{1,99} = 7.3$; $p < 0.01$) concentrations in the sediment (Figure 7c-d). However, these relationships depended on the wrack species considered (i.e. wrack: abundance interaction, Table 3). Thus, the macrofauna-OM relationship ($F_{4,90} = 3.2$; $p < 0.05$) was stronger in Up than in the other types of wrack patches (Figure 7c, Table 3). The macrofauna-NH_4^+ relationship ($F_{4,88} = 6.5$; $p < 0.001$) was also stronger in Up than in the Cb and Sp patches (Figure 7d, Table 3).

4. Discussion

The role of beaches as metabolic hotspots and that of wrack as a source of CO_2 are poorly studied topics (Coupland and others 2007). Here we demonstrate the active

363 metabolic role of beach wrack and how different algal species support different wrack
364 respiration rates.

365 **4.1. Wrack degradation and metabolic activity**

366 The biomass of all algae decreased rapidly throughout the study period, following a
367 typical wrack decomposition pattern (e.g. Olabarria and others 2007; Rodil and others
368 2008). However, the algal biomass differed after 12 days, indicating a species-specific
369 mass loss. Thus, the weight loss was greater in *S. polyschides* and *U. pinnatifida* patches
370 than in *S. muticum* and *C. baccata* patches. Our results also showed that beach wrack was
371 metabolically very active, and supported intense CO_2 fluxes, thus confirming the findings
372 of a previous study also conducted on beach-cast metabolic rates (Coupland and others
373 2007). Thus, wrack supported higher respiration rates than bare sediments, with some
374 patches showing higher rates than reported for other wrack species (Coupland and others
375 2007). Our findings indicate that beach wrack deposits act as metabolic hotspots, as
376 observed in other major ecosystems around the world, including land communities, such as
377 tropical rain forests, and seafloor communities, such as seagrass meadows (see Coupland
378 and others 2007 for explicit comparisons). In contrast to the latter study, we show that
379 wrack differing in species composition had different metabolic rates, indicating a
380 differential species-specific metabolic activity. For instance, metabolically reactive *S.*
381 *polyschides* and *U. pinnatifida* are structurally simple algal species with long, labile strap-
382 like blades that stack up in layers on the sand and that degrade rapidly and become readily
383 available for consumption. *S. muticum* and *C. baccata* are morphologically more complex
384 algae with resistant leathery branches bearing secondary branches that slow down their
385 degradation, so that they remain for longer on the beach. Some marine vegetation, such as
386 seagrass, with large and robust structures and known to be resistant to degradation, contain
387 refractory organic matter components that are resistant to degradation and microbial attack

388 (Trevathan-Tackett and others 2017). Similarly, wrack structure (shape and toughness) is
389 important in relation to algal-specific biochemical composition (nutrients and phenols) and
390 variable surface:volume ratio in the sediment (e.g. Duggins and Eckman 1997; Bucholc
391 and others 2014).

392 **4.2. Effects of wrack patches on sedimentary nutrients and community structure**

393 High levels of sedimentary nutrients associated with the remineralization of wrack were
394 recorded, suggesting rapid leaching from the wrack (Dugan and others 2011). Nutrient
395 variability in the beach sediments is often related to different types of accumulations found
396 on the shore (Dugan and others 2011; Barreiro and others 2013). For instance, structurally
397 simple algae with the potential to store large quantities of nutrients can cause rapid
398 leaching of nutrient compounds during decay (Hanisak 1993; Barreiro and others 2013).
399 Thus, *U. pinnatifida* provided the greatest amounts of organic matter, probably due to the
400 rapid decay. Similarly, the greatest contributions of nitrate and nitrite (i.e. NO_x^--N) were
401 associated with *S. polyschides* and *U. pinnatifida*. High levels of NO_x^--N suggest rapid
402 nitrification of the NH_4^+ derived from remineralized wrack (Dugan and others 2011).
403 Release of large amounts of PO^{-3}_4 was also associated with *U. pinnatifida*. The rapid
404 release of inorganic nutrients during algal mineralization is ecologically relevant because
405 these compounds represent a main source of nutrients for microbes and macrofauna (Malm
406 and others 2004; Ince and others 2007).

407 The decomposition of wrack and the consequent leaching of the organic matter into the
408 underlying sediment require the joint action of microbial decomposers and detritivores
409 (Koop and Griffiths1982; Inglis 1989; Dugan and others 2003, 2011). For instance, the
410 dissolved inorganic nitrogen (DIN) stored in the sediments beneath wrack may be
411 associated with degradation and consumption of the wrack by respectively bacteria and
412 macrofauna (Orr and others 2005). Thus, the strong positive relationship between DIN and

413 bacteria in the experimental wrack patches supports the role of bacteria as key
414 decomposers of wrack (Koop and others 1982; García-Robledo and others 2008; Sosik and
415 Simenstad 2013). In our study, large numbers of bacteria rapidly colonized the wrack, and
416 bacterial assemblages varied significantly, possibly due to the specificity of bacteria
417 associated with different algae (Barott and others 2011). The activity of bacterial strains
418 consisting of several genera with diverse capacities poses an advantage in the presence of
419 different wrack. Thus, the relationship between DIN and bacteria observed in the patches
420 may reflect aerobic respiration by autotrophic bacteria (García-Robledo and others 2008).
421 The rapid rate of degradation and greater nutrient releases from *S. polyschides* and *U.*
422 *pinnatifida*, together with significant DIN-bacteria relationships, indicates the need for
423 studies with higher sampling frequency (i.e. daily or even hourly). This type of studies
424 would provide more accurate information on nutrient release and a more detailed response
425 of the benthic community to the wrack biomass.
426 The beach macrofauna community is capable of quickly processing detritus and linking
427 oceanic productivity to upper-trophic consumers (Dugan and others 2003). For instance,
428 the organic matter and NH_4^+ concentrations under *U. pinnatifida* were significantly and
429 positive related to the presence of macrofauna. This macroalgal species degrades quickly
430 and is very rich in nutrients that are readily available to consumers and essential for
431 various metabolic functions (Sánchez-Machado and others 2004; Park and others 2012).
432 The beaches under study showed contrasting community structure and colonization
433 patterns related to the beach life-history that affected the potential relationships between
434 wrack biochemical composition and associated consumers. Thus, on AM the typical
435 macrofauna were only found at the end of the experiment, and even then, the associated
436 macrofauna assemblage was dominated by dipteran larvae. Conversely, typical wrack-
437 associated talitrids were only present on AB, facilitating degradation of the wrack and

consequently the beach nutrient cycling. Talitrids were most abundant in the *S. muticum* and *C. baccata* patches on AB. This is probably related to the potential benefits provided by the structurally complex macroalgae (long-lasting refuge from predation and environmental stress) as an alternative habitat for the fauna (e.g. Cowles and others 2009).

AM beach is subjected to regular mechanical grooming that removes wrack and modifies the community, while no cleaning activities are carried out at AB. Beach grooming is known to modify the role of the beach microbial community through changes in bacterial production in the underlying sand and in the associated surf zone that can affect the microbial food-web and even the water quality (Malm and others 2004; Russell and others 2014). Removing wrack from beaches potentially alters local benthic communities (Dugan and others 2003). The lack of talitrids on AM, combined with regular and intense beach grooming, may have created a situation where the presence of wrack triggered the oviposition of dipteran larvae, leading to an increase in the presence of flies. This represents an important change in the beach community scenario from a typical beach fauna to a terrestrial community type.

4.3. Ecological implications

The role of detrital subsidies on sandy beach communities can be affected in a future scenario of global change. For instance, climate change may alter the amount and identity of the macroalgae growing offshore affecting how much, and the kind of wrack, is deposited on intertidal shores worldwide (e.g. Bishop and others 2010; Byrnes and others 2011; Krunhshal and Scheibling 2012; Rodil and others 2015a). As global climate change factors increase wrack production (Smetacek and Zingone 2013) and introduced algae spread worldwide (Williams and Smith 2007), unwanted piles of wrack will be cast ashore thus affecting coastal goods and services and challenging the coastal functioning. For instance, *U. pinnatifida* and *S. muticum* are highly invasive and colonize coastal areas

463 worldwide, thus potentially influencing benthic communities and food-webs on coastal
464 shores (e.g. Rodil and others 2008; Suárez-Jiménez and others 2017). In some areas of the
465 world, the increasing development of massive *Sargassum* spp. shore-accumulations (i.e.
466 golden tides) is known to affect tourism-based economies (Smetacek and Zingone, 2013).
467 However, moderate accumulations of specific species of wrack, including non-native
468 species, may have a positive role on beach communities as trophic deposits (Olabarria and
469 others 2009; Quijón and others 2017; Suárez-Jiménez and others 2017). Here, we show
470 that wrack can represent an important source of beach metabolic activity, depending on the
471 type of wrack that accumulates on the beach. Consequently, large wrack accumulations of
472 specific algal species can promote high emissions of CO_2 (Coupland and others 2007; the
473 present study), potentially affecting the functioning of land-sea interfaces. For instance, the
474 high carbon-to-nitrogen ratio (50:1) of *Sargassum spp.* makes this alga a very efficient
475 vehicle for sequestering carbon in the oceans (Smetacek and Zingone 2013). *U. pinnatifida*
476 can also contribute to increasing the carbon export to nearby ecosystems and can alter the
477 biomass export regime as it spreads across shallow coastal habitats (Tait and others 2015).
478 Therefore, increasing accumulations of wrack emitting CO_2 into the atmosphere from
479 intertidal shores can affect the role of macroalgae in marine carbon sequestration (Krause-
480 Jensen and Duarte 2016). The potential influence of beach wrack in the global carbon
481 balance, mainly during seasonal peaks in accumulation, has not generally been considered
482 and deserves further detailed study. The capacity of beaches as metabolic hotspots and
483 wrack as a source of CO_2 adds further value to the many ecological services provided by
484 beach systems. Significant modifications in the quality (non-indigenous species) and
485 quantity (beach grooming/seaweed tides) of beach wrack may change fundamental
486 processes related to the marine-terrestrial transfer of nutrients and energy, and to the
487 marine-atmospheric transfer of greenhouse gas emissions.

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660

661 **Table 1.** Summary showing the mean ± standard error of the metabolic activity (μmol CO_2 μm^{-2} s^{-1}) of all the wrack species ([a]wrack patches averaged
662 over time) and per sampling day ([b]time averaged for all the wrack species) from the two study beaches (AM: América and AB: Abra). We also show
663 maximum and minimum values, and the cumulative sum of the CO_2 flux per sampling time (12 days for AM, 6 days for AB) and wrack species.

Beach	Wrack species[a]	Mean±SE	Maximum	Minimum	Cumulative	Time[b]	Mean±SE	Maximum	Minimum
AM	*S. polyschides*	3.4±0.6	8.98	0.71	13.8	time 0	0.9±0.1	1.65	0.04
	U. pinnatifida	6.5±0.9	11.2	1.33	25.8	time 3	2.6±0.7	9.94	0.04
	C. baccata	1.4±0.2	2.26	0.51	5.5	time 6	4.2±0.9	11.2	0.07
	S. muticum	2.7±0.6	8.01	0.36	10.8	time 12	3.6±0.6	8.01	0.07
	Sand control	0.07±0.02	0.11	0.04	0.3				
AB	*S. polyschides*	4.7±0.9	8.07	0.60	14.2	time 0	1.0±0.13	1.90	0.10
	U. pinnatifida	8.3±1.5	14.9	1.50	24.9	time 3	3.95±0.9	12.0	0.10
	C. baccata	1.5±0.2	2.40	0.80	4.5	time 6	5.1±1.0	14.9	0.10
	S. muticum	2.1±0.3	3.90	0.90	6.4	time 12	-	-	-
	Sand control	0.09±0.03	0.13	0.05	0.3				

664 **Table 2.** *A posteriori* comparisons (posthoc tests, lsmeans) on the effects of wrack
665 patches, beach (AM: América, AB: Abra) and time (0, 3, 6 and 12 days) on wrack
666 metabolic activity (CO_2: µmoles m^{-2} day^{-1}) after a 3-way ANOVA analysis (see
667 supplementary material Table S2).

Wrack patch	Beach	posthoc tests ($p < 0.001$)
S. polyschides (Sp)	AM	t6 > t12 = t3 > t0
	AB	t0 < t3 < t6
U. pinnatifida (Up)	AM	t0 < t3 = t6 = t12
	AB	t0 < t3 = t6
C. baccata (Cb)	AM	t0 = t3 < t6 = t12
	AB	t6 > t0 = t3; t3 = t6
S.muticum (Sm)	AM	t0 = t3 = t6 < t12
	AB	t0 = t3 < t6
Sand control	AM	t0 = t3 = t6 = t12
	AB	
Time		
0	AM	Sand < *Cb* < *Up* =*Sm*; *Cb* = *Sp*; *Up* =*Sm* = *Sp*
	AB	Sand < *Cb* = *Sp*; *Sp* = *Sm*; *Cb* < *Up*
3	AM	Sand < Sm = Cb < Sp < Up
	AB	Sand < Sm = Cb < Sp = Up
6	AM	Sand < *Sm* = *Cb* < *Sp* = *Up*
	AB	
12	AM	Sand < *Cb* = *Sp* < *Sm* = *Up*

668

669 **Table 3.** Summary of the generalized linear models indicating the significance of macrofauna abundance on wrack-related response variables

670 (OM: organic matter (%), NH_4^+: ammonium (µM)), including significant pair-wise contrasts between patches (Sp: *S. polyschides*, Up: *U.*

671 *pinnatifida*, Cb: *C. baccata*, Sm: *S. muticum*).

	Model summary (G_ZLM)						
Regression-based models	Coefficient	Estimate	$t^{(p)}$	Contrasts	Estimate	$t^{(p)}$	pseudo-R^2
OM ~ Patch:Abundance[a]	Cb:Abundance	0.001	0.67	Cb-Up	0.007	3.24^{**}	29.2
	Sm:Abundance	0.0001	0.04	Sm-Up	0.007	2.5^{*}	
	Sp: Abundance	0.001	0.69	Sp-Up	0.006	2.9^{*}	
	Up: Abundance	0.01	4.35^{***}				
NH_4^+ ~ Patch: Abundance[a]	Cb:Abundance	-0.22	-1.28	Cb-Up	1.5	4.8^{***}	35.1
	Sm:Abundance	0.50	1.44	Sp-Up	1.1	3.3^{**}	
	Sp: Abundance	0.20	0.80	Sm-Up	0.75	1.7^{+}	
	Up: Abundance	1.30	4.9^{***}	Cb-Sm	0.72	1.9^{+}	

[a]Negative binomial model distribution (log-link structure) to avoid overdispersion.
Proportional increase in explained deviance: pseudo-R^2.
Significance: $^{***}p < 0.001$; $^{**}p < 0.01$; $^{*}p < 0.05$; $^{+}0.05 < p < 0.10$.

672 **Figure captions**

673 **Figure 1.** Mean (+SE) amount of (a) wrack biomass over time and (b) among algal
674 species, (c) wrack temperature at the beaches over time, (d) sedimentary organic matter
675 between patches and over time, (e) sedimentary water content at the beaches and (f)
676 between wrack patches (time-accumulated). Beaches (América, AM, and Abra, AB),
677 wrack (*S. polyschides Sp, U. pinnatifida Up, C. baccata Cb, S. muticum Sm,* and procedure
678 sand control PC) and time (3, 6 and 12 days). Data are displayed per significant factors
679 (non-significant factors are averaged, see Table S1).

680 **Figure 2.** Mean (+SE) amount of sedimentary NO_2^-, NO_3^-, NH_4^+ and PO_4^{3+} underneath the
681 experimental wrack patches (*S. polyschides Sp, U. pinnatifida Up, C. baccata Cb, S.*
682 *muticum Sm,* and procedure sand control PC) at the beaches (América, AM, and Abra,
683 AB). Data are displayed per significant factors (see Table S2).

684 **Figure 3.** Mean (+SE) amount of sedimentary NO_2^-, NO_3^-, NH_4^+ and PO_4^{3+} underneath the
685 experimental wrack patches (*S. polyschides Sp, U. pinnatifida Up, C. baccata Cb, S.*
686 *muticum Sm,* and procedure sand control PC) over time (3, 6 and 12 days). Data are
687 displayed per significant factors (see Table S2).

688 **Figure 4.** Mean (±SE) wrack metabolic activity (i.e. CO_2) at the beaches (América and
689 Abra) compared between wrack patches (*S. polyschides Sp, U. pinnatifida Up, C. baccata*
690 *Cb, S. muticum Sm,* and procedure sand control PC) over time (0, 3, 6 and 12 days). Data
691 are displayed per significant factors (see Table 2 and Table S2).

692 **Figure 5.** Mean (+SE) wrack-associated (a) bacterial richness (operational technical units),
693 and (b) macrofauna taxa at the beaches over time, (c) total macrofauna abundance
694 (counts), (d) Anthomyiidae abundance at the beaches (AM and AB) and (e) talitridae
695 abundance between wrack patches (AB beach). Beaches (América, AM, and Abra, AB),
696 wrack (*S. polyschides Sp, U. pinnatifida Up, C. baccata Cb, S. muticum Sm,* and procedure

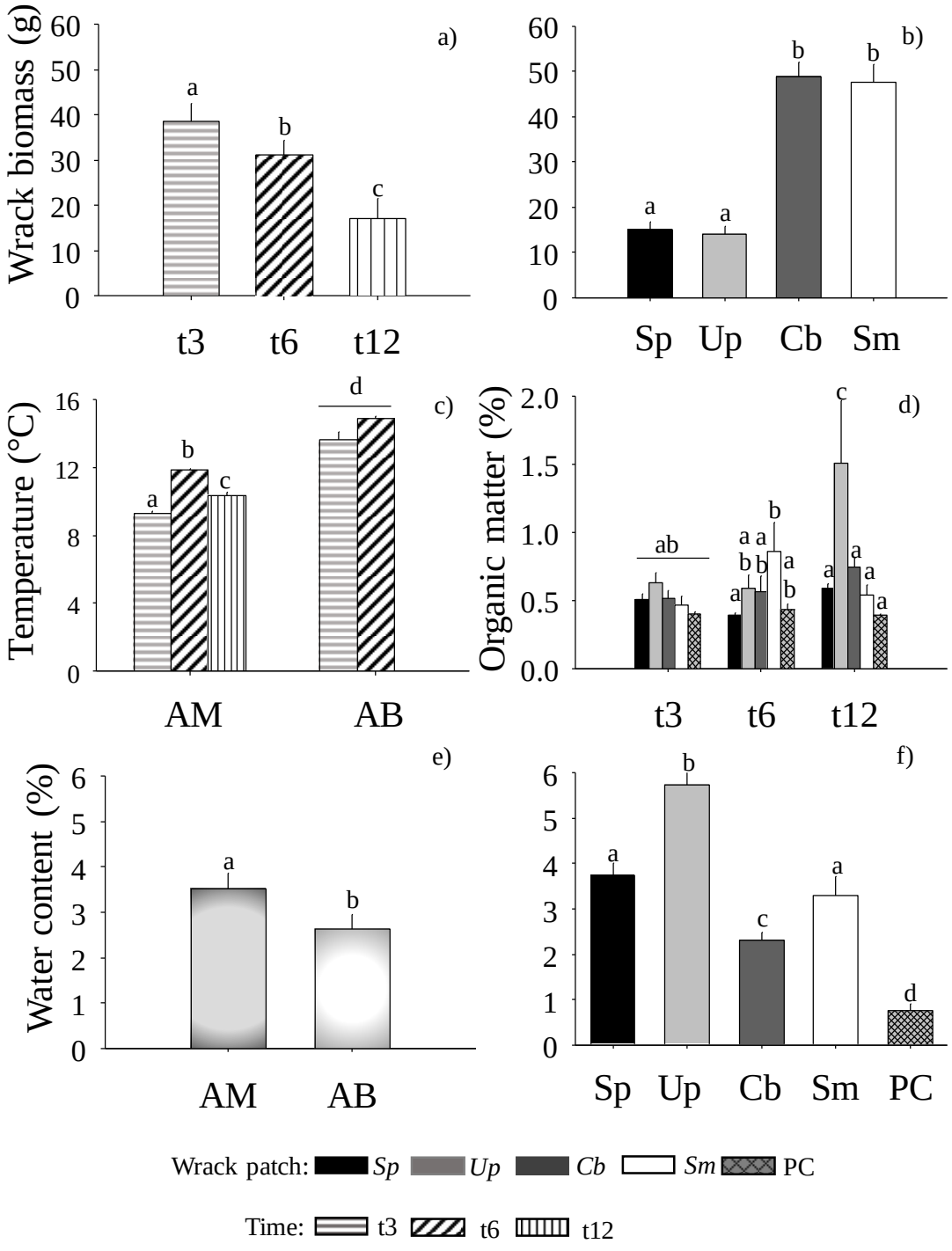
697 sand control) and time (3, 6 and 12 days). Data are displayed per significant factors (non-
698 significant factor are averaged, see Table S4).

699 **Figure 6.** Non-metric multidimensional scaling (nMDS) for differences in bacterial
700 assemblages between beaches (América, AM, and Abra, AB), wrack (*S. polyschides Sp*, *U.*
701 *pinnatifida Up*, *C. baccata Cb*, *S. muticum Sm*, and procedure sand control, PC), and over
702 time (3, 6 and 12 days).

703 **Figure 7.** Responses of the (a) wrack biomass (dry weight) to bacterial richness (OTUs),
704 (b) sedimentary total dissolved inorganic nitrogen concentration (DIN) to bacterial
705 diversity (Shannon-diversity), and responses of the sedimentary (c) organic matter and (d)
706 ammonium (NH_4^+) concentration to macrofauna abundance. Wrack patches: *S.*
707 *polyschides*, Sp; *U. pinnatifida*, Up; *C. baccata*, Cb; *S. muticum*, Sm.

708 Figure 1.

709



710

Figure 2.

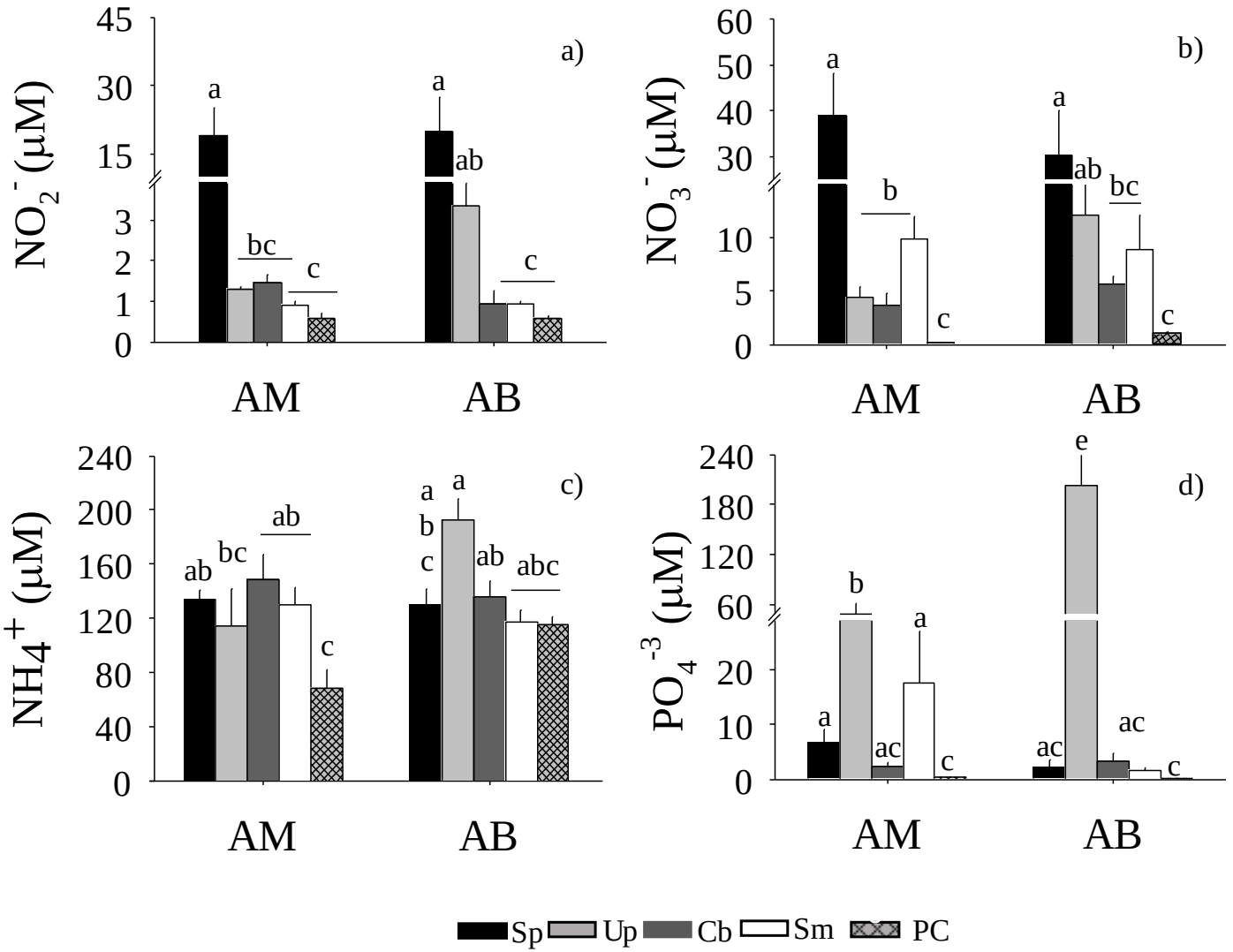
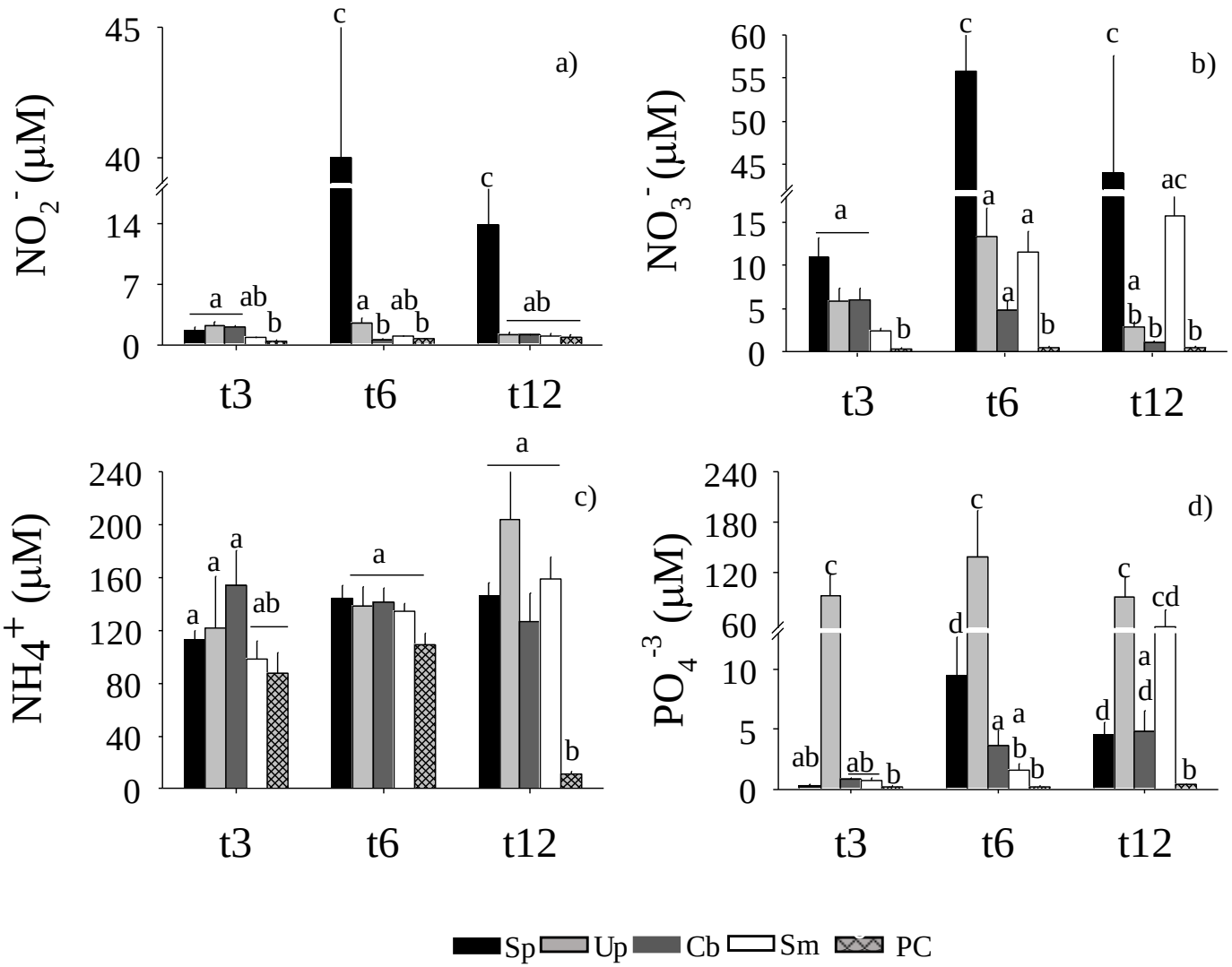
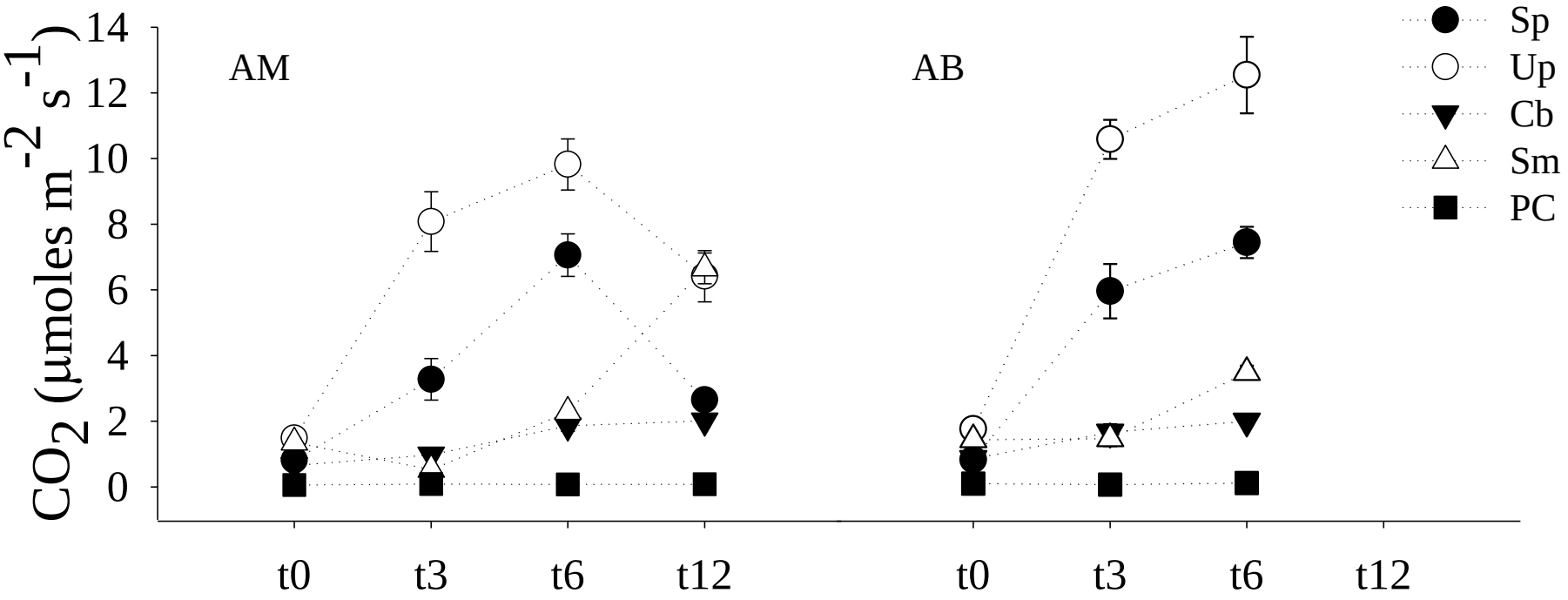


Figure 3.



741 Figure 4.



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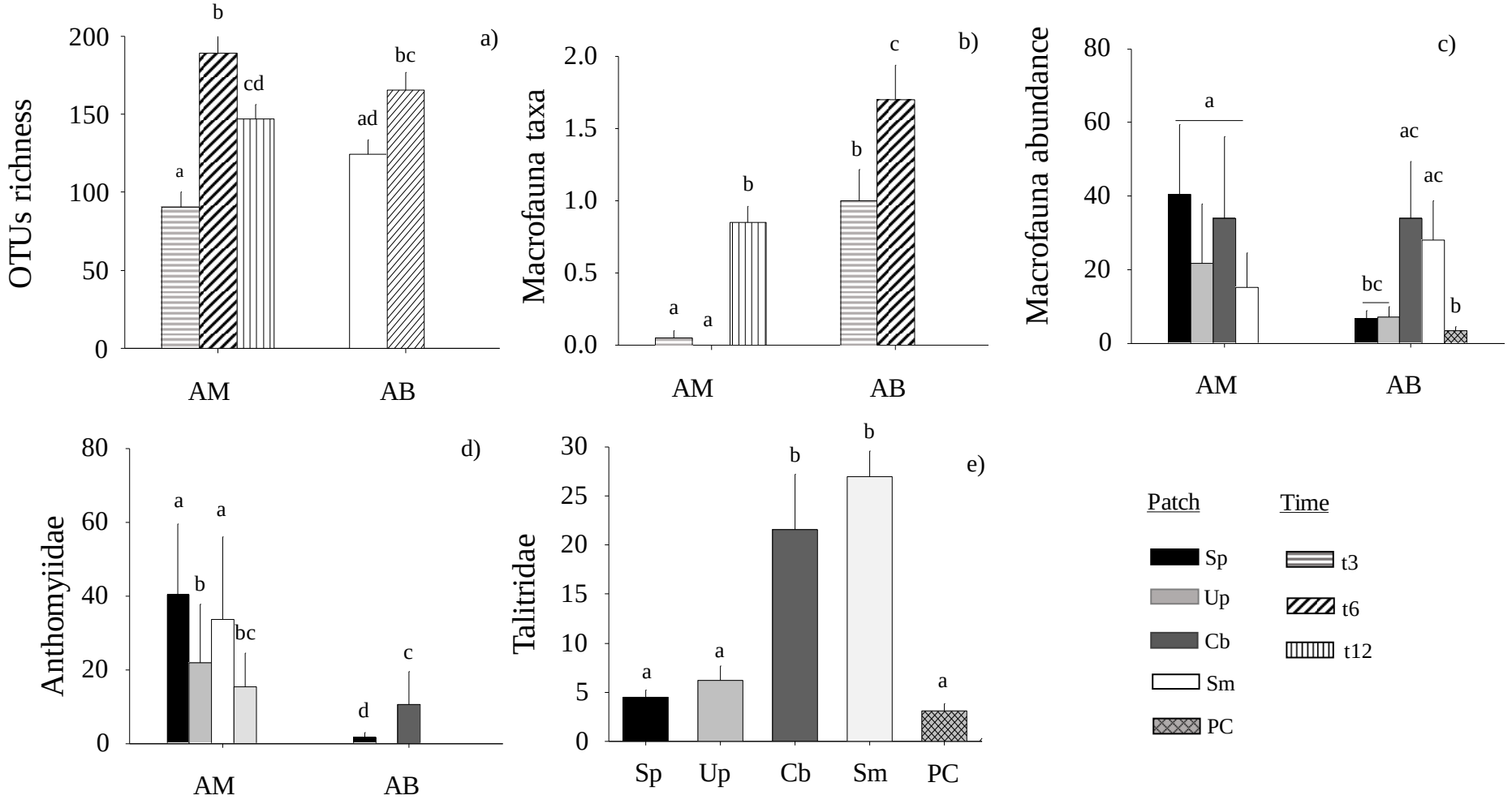
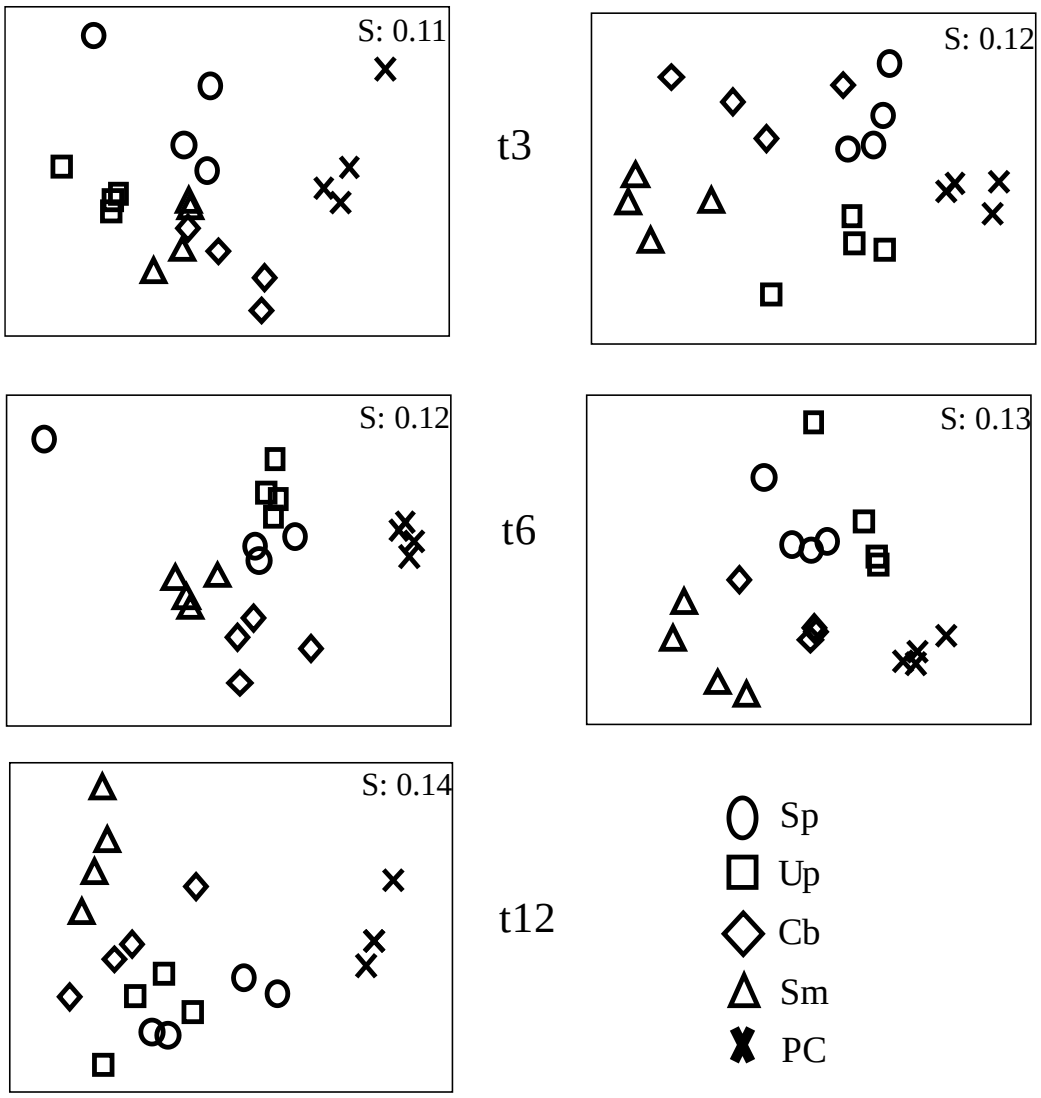
747 Figure 5.


a)
OTUs richness
200
150
100
50
0
a
b
cd
ad
bc
AM
AB
b)
Macrofauna taxa
2.0
1.5
1.0
0.5
0.0
a
a
b
b
c
AM
AB
c)
Macrofauna abundance
80
60
40
20
0
a
bc
ac
ac
b
AM
AB
d)
Anthomyiidae
80
60
40
20
0
a
b
a
bc
d
c
AM
AB
e)
Talitridae
30
25
20
15
10
5
0
a
a
b
b
a
Sp
Up
Cb
Sm
PC
Patch
Sp
Up
Cb
Sm
PC
Time
t3
t6
t12

748 Figure 6.



749 Figure 7.

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